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# POLYRHACHIS SIMPLEX
# THE WEAVER ANT OF ISRAEL (*)

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## *SUMMARY*

The Weaver Ant, *Polyrhachis simplex,* which in India belongs to a tropical fauna, occurs in Israel in a circumscribed desert region which comprises the western limit of its spread. The biology of *P. simplex* features a number of highly interesting phenomena :

1. *Weaving* occupies a central position in the life of the colony. The workers construct the nests with the aid of silk secreted by the larvae. The silk glands of the larva are consequently highly developed.
2. *Aphids* of several species are visited by the weaver ant for their honeydew, which constitutes a primary food source for the ant.
3. *Seasonal vertical migration* of the ants occurs twice a year—in the winter and in the late spring.
4. « *Cemeteries* » are marked off by the ants at considerable distances from the nests, for the purpose of disposing of their dead. A single « cemetery » may serve several widely-separated ant colonies.

The present investigation is the first in which colonies of *P. simplex* have been successfully reared in the laboratory, using a special sugar solution as a substitute for the natural food of the ants. The laboratory-reared colonies developed normally, maintained the usual daily activities (including weaving) and reproduced through several generations.

## *RÉSUMÉ*

La fourmi fileuse, *Polyrhachis simplex,* qui appartient en Inde à une faune tropicale, se rencontre en Israël dans une région désertique correspondant à la limite occidentale de son extension.

La biologie de cette espèce présente un certain nombre de caractères intéressants :

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1° Le filage tient une place de premier ordre dans la vie de la colonie. Les ouvrières construisent les nids à l'aide de la soie sécrétée par les larves et en conséquence les glandes séricigènes de ces dernières sont très développées.

2° Des Aphidiens de plusieurs espèces sont visitées par les ouvrières qui trouvent dans le miellat une source importante de nourriture.

3° Une migration saisonnière verticale a lieu deux fois par an, en hiver et à la fin du printemps.

4° Des « cimetières » sont constitués par les fourmis à des distances considérables des nids afin d'y déposer les cadavres. Un seul « cimetière » peut être utilisé par plusieurs colonies bien séparées.

Au cours de cette étude, il a été possible, pour la première fois, d'élever des colonies de cette espèce au laboratoire en utilisant une solution de sucre particulière au lieu de la nourriture naturelle. Les colonies élevées au laboratoire se développaient normalement, maintenaient leur activité journalière (y compris le filage) et se sont reproduites durant plusieurs générations.

## INTRODUCTION

There are three distinct phytogeographical regions within the boundaries of Israel and each has its typical climate, soil and flora.

The Northern part of the country is predominantly under the influence of the Mediterranean Sea; the Central part is infiltrated by the Irano-Turanian Steppe region, and the Southern part has mostly a Saharo-Sindic Desert character (ZOHARY, 1955). Variability of the terrain is well reflected in the flora and fauna of the country and its influence is recognisable also on the local ant population.

The ant population boasts a wealth of species and subspecies, and includes also the Tropical species *Polyrhachis simplex*. The latter species is widespread in enclaves within the desert region of the country which are rich in fresh water and tropical vegetation. The largest of these enclaves is the Ein-Gedi oasis, which is situated in the Judea Desert near the Dead Sea. The other enclaves are small and occur about freshwater springs. They are all part of a large phytogeographical region extending from the Sahara Desert and the Sudan to the Deccan area of India. The phytogeographical bond linking theses enclaves also creates a faunal bridge between *P. simplex* of Israel and the Indo-Malayan mother fauna.

Representatives of *P. simplex* which inhabit the banks of the Arugot Stream near Ein-Gedi are well-known for their weaving ability—a skill which has earned this species the title of Weaver Ant.

The species *P. simplex* and in fact genus *Polyrhachis* as a whole, has been very little investigated. This is rather surprising insofar as the genus comprises over 300 species, most of them « weavers ».

According to WASMANN (1905, Wronghton was the first to study the genus *Polyrhachis*, and his observations on a number of species from East India were published in 1892 under the title *Our Ants*. He was followed by FOREL, who in 1894 described a nest of *P. simplex* from India. LEFROY and HOWLETT (1909) observed the weaving of *P. simplex* and recognising the connexion between this species and aphids they called the latter « ant cows ». HINGSTON (1923) expanded the knowledge on ant-aphid interrelations and dwelled particularly on the manner of construc

tion of the « byres ». KARAWAJEW (1929) studied the anatomy of the larvae of some *polyrhachis* species (other than *P. simplex*) and found a positive correlation between quality of the weave and state of development of the silk glands in the larvae of the various species.

In the present paper, additional observations are made on the biology of *Polyrhachis simplex*. The data have been collected both from field studies of the ant in its natural biotope as well as from artificial cultures raised in the laboratory.

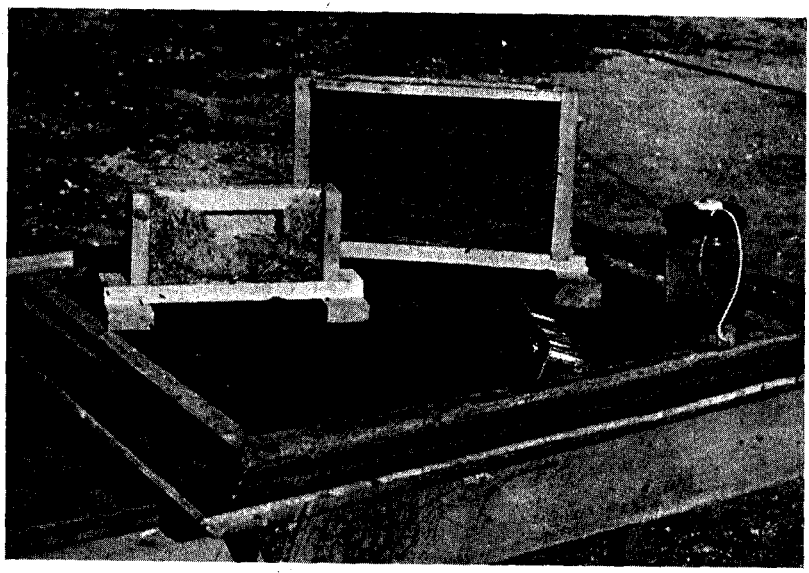

FIG. 1. — Large table for raising *Polyrhachis simplex* colonies in the Laboratory. On the surface of the table can be seen :

*a)* Large vertical breeding house with shutters down (centre) ;
*b)* Small vertical breeding house, with front removed to show the weave inside (left) ;
*c)* Feeding apparatus (front) ;
*d)* Drinking apparatus (right).

Table is surrounded by metal water trough.

## MATERIAL AND METHODS

The present investigation extended over a period of three years, and as already pointed out, it comprised both field and laboratory observations. During 1964/5, monthly visits were made to the Arugot Stream, where the largest concentration of weaver ants could be found. Here the ecological conditions of the biotope were studied and a survey was made on the ant population and the seasonal distribution of their nests. The daily activities of the ants throughout the year were also investigated. A considerable part of the field observations was devoted to a study of the

interrelations between weaver ants and the aphids which supply most of their food. During the years 1965-7, the investigation was expanted to cover other distribution sites where weaver ants had been discovered.

In parallel to field studies of the weaving ant, colonies of this insect were also reared in the laboratory to enable unhindered, controlled observations such as are not obtainable in nature. In view of its important role in the colony, the primary target of laboratory study was the larva of *P. simplex*—its activity, morphology and anatomy, and also the structure of its silk. For the purpose of laboratory study, the following equipment was used :—

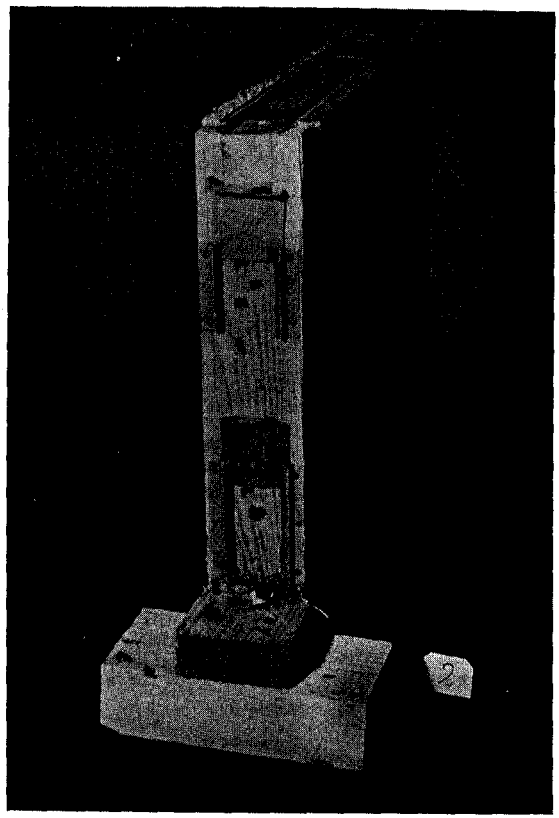

FIG. 2. — Large vertical breeding house; side view showing entrance (bottom) and ventilation holes (centre and top).

1. *Large Table* (fig. 1). — Surrounded on all sides by a metal drainpipe acting as a water trough. The table serves several purposes : *a)* It isolates the colony without interfering with the normal ant activities; *b)* it enables undisturbed observations; and *c)* it has a water-filled drainpipe substituting for a natural freshwater stream.

2. *Breeding Houses.* — Breeding houses made mainly of wood have proven efficient and fully suitable to the needs of the weaver ant. Three types were used :—

a) *Horizontal.* — On the one side of a thin plywood board, 15 × 10 cm, is fitted a narrow, 8 mm thick, wooden frame with a small aperture at one corner. A glass plate of dimensions equal to those of the plywood board, is fastened onto the wooden frame and held tight with rubber bands, this forming a narrow, rectangular box of sufficient volume for a medium-sized colony. This type of breeding house is easy to construct, allows comfortable observation and is also portable. During the migratory period (Vide *infra*), it also serves as an ant trap.

b) *Vertical.* — As shown in figure 2, this breeding house resembles a miniature model hive. Its dimensions are 33 × 22 × 4.5 cm. On both sides of the breeding house are fitted transparent glass plates which serve as windows through which the interior may be viewed. These plates are replaceable once they become coated with silk. The frame in front of each window is slotted to house a sliding ply-

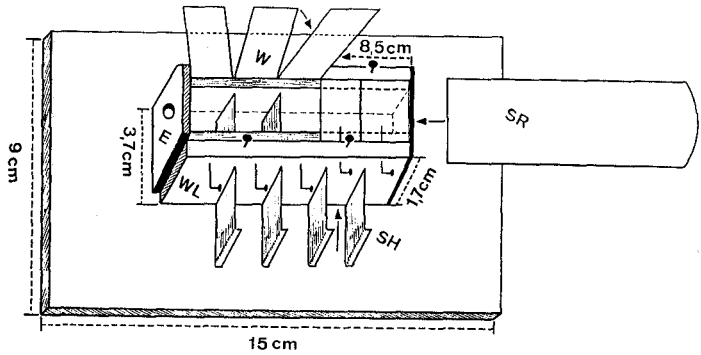


FIG. 3.

Experimental Observation Chamber (schematic) : *e*, entrance; *sh*, shutter (tin); *sr*, sliding roof (cardboard); *w*, window (glass); *wl*, window latch (ordinary pin).

wood shutter. When desirable, the shutters may be closed to darken the interior of the breeding house. The latter has two entrances and 6 ventilation holes, with facilities for temperature regulation.

c) *Observational* (fig. 3). — An observation chamber was built for small-scale, brief observations. It was used to observe the mating process (fig. 4) and subsequently—oviposition by the queen, development of the larvae and so on. The observation chamber has tiny glass windows and a clear glass floor the size of a microscope slide. These allow rapid examination also with the aid of instruments. Slidling tin shutters divide the chamber into 5 compartments, so that several objects may be isolated concurrently for observation.

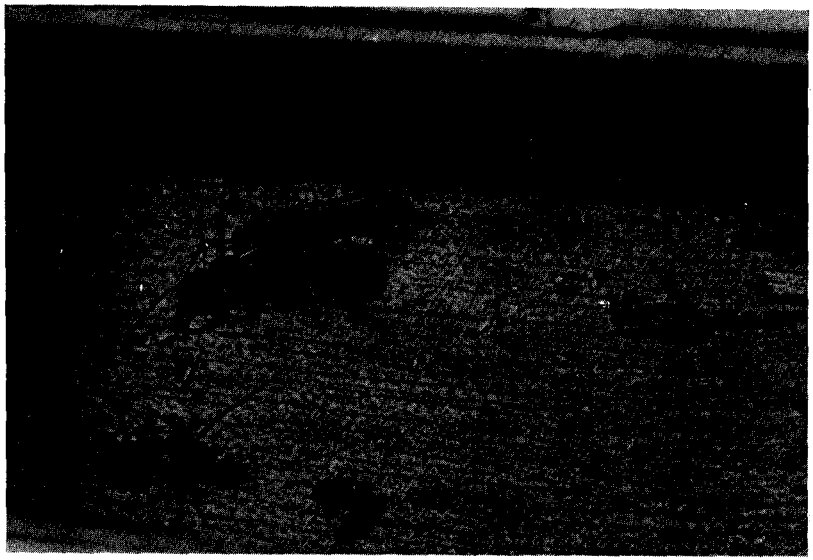

FIG. 4. — *Polyrhachis simplex* in copula (top centre) inside Observation Chamber.

3. *Feeding Apparatus* (fig. 5). — A food substitute for aphid secretion was derived

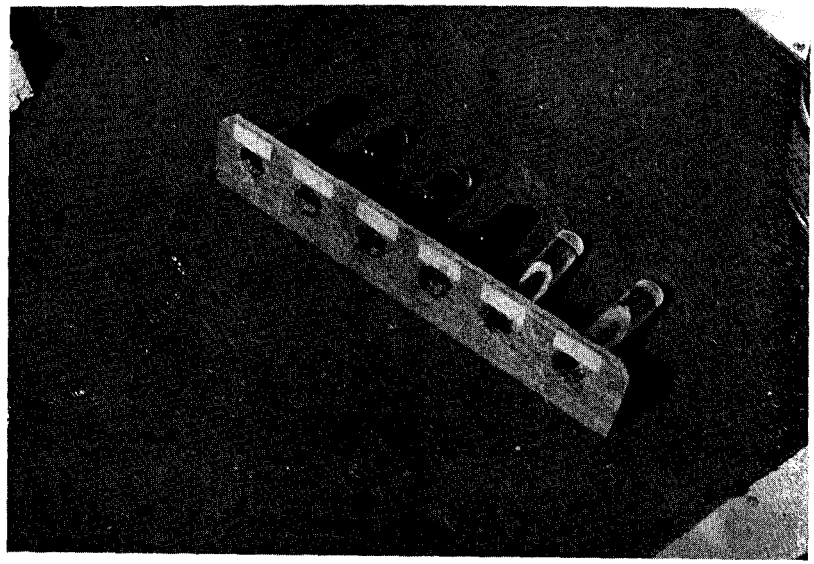

FIG. 5. — Feeding Apparatus for *Polyrhachis simplex* colonies, with facilities for various sugar solution concentrations.

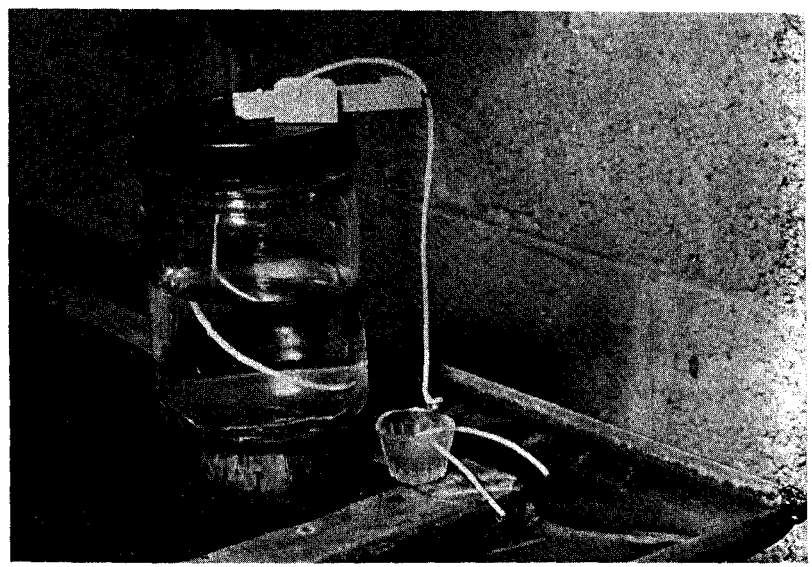

FIG. 6. — Drinking Apparatus (see text for explanation).

experimentally for the laboratory feeding of the ants. The nutrient found most suitable was an aqueous solution of 15 % sucrose + 1 % NaCl. The feeding apparatus for liquid food was modelled after in the jar (1 liter) can last for as much as a week. An added advantage of the siphon is that it prevents drowning of ants while drinking and thus eliminates contamination of the water.

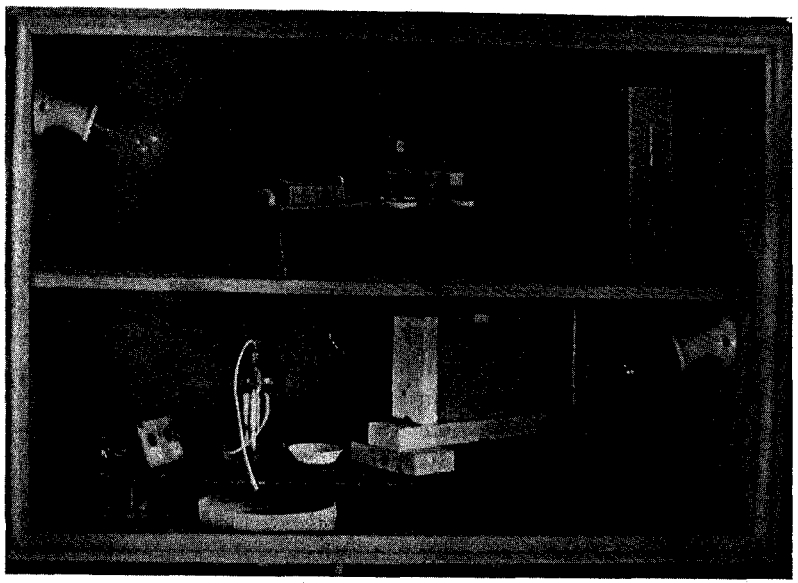

FIG. 7. — Incubator for raising weaver-ant colonies : Front view with window removed.

SKAIFE (1961). In addition to the mentioned nutrient solution, the ants were offered adult insects or other arthropods as a source of proteins.

4. *Drinking Apparatus* (fig. 6). — The problem of providing the colony with a constant supply of clean drinking water was solved by the use of a siphon, as shown in the Figure. With proper constriction of the capillary tube, the quantity of water

5. *Incubator* (fig. 7). — Raising of weaver ants far from their natural habitat necessitates a strict maintenance of suitable temperature. A solution to this problem was keeping the colony in an incubator, of the following dimensions : 80 × 40 × 50 cm. Two light bulbs of 75W each, provide the necessary heat. Sliding glass panes cover the front of the incubator and permit regulation of the temperature inside.

## WORLD DISTRIBUTION OF THE WEAVER ANT

FOREL (1923) divides the world population of ants into 11 faunas. According to this division, the weaver ant belongs to the Indo-Malayan fauna, which ranges over a large part of India and over Ceylon, Indochina, Southern China, Southern Japan, the Andaman and Nicobar Islands, Sumatra, Java and the Philippines. According to BINGHAM (1903), the weaver ant is widespread in Burma, India, Ceylon and other areas. FOREL (1910) was first to report the existence of the weaver ant in the vicinity of the Dead Sea, although he did not specify any exact location. EMERY (1925) added a list of new habitats, mentioning Iraq and Transjordan. It is interesting to note that the last-mentioned countries, namely, Palestine (now Israel), Iraq and Transjordan (now Jordan), do not belong to the zone of the Indo-Malayan fauna but rather to that of the East Mediterranean subfauna. Israel, in fact, is included in the zone of Palearctic fauna, which borders the zone of Indo-Malayan fauna. FOREL (1923) does, however, point to a great similarity between this sub-fauna and a desert sub-fauna which occurs in India. Consequently he finds it easy to understand how the weaver ant spread from India to Asia Minor and from there—to the East-Mediterranean countries. MENOZZI (1933) and FINZI (1936) studied the ant fauna of the Near East and reported the presence of the weaver ant in Transjordan, Palestine and Sinai. COLLINGWOOD (1960) extended the range of the weaver ant as far north as Afganistan. BYTINSKI-SALZ (1953), in his study on the zoogeography of ants in the Middle East, considers the weaver ant as a Paleotropic element, i.e., as a tropical element which had penetrated the Palearctic region from Eastern India, much the same as other tropical elements had penetrated from the south via Sudan and Ethiopia.

From all the above, it is clear that the species *P. simplex*, like the entire genus *Polyrhachis*, has its main spread within tropical regions, even though it does penetrate another fauna. Its range has Israel and Sinai as its westernmost limit and here, also, the weaver ant finds its lowest habitat, namely, the region of the Dead Sea, which is 392 meters below sea-level. Its highest habitat to date is in Afganistan, where it is encountered at an altitude of 900 meters above sea-level.

## DISTRIBUTION OF THE WEAVER ANT IN ISRAEL

Scientists and nature-lowers who participate in educational guided tours to the Arugot Stream near Ein-Gedi, are well acquainted with the weaver ant. The Arugot Stream, however, is not the only habitat of this insect—other sites have been discovered since the beginning of the present study, and the limits of its distribution are now known to extend southwards till Ein-Erga (near the Ein-Yahav Settlement) and westwards till the Avdat Stream. Water sources, usually springs, are common in all sites of occurrence of the weaver ant. As for the vegetation, part or all of the plants which, at the Arugot Stream, host aphids and attract the weaver ant, occur

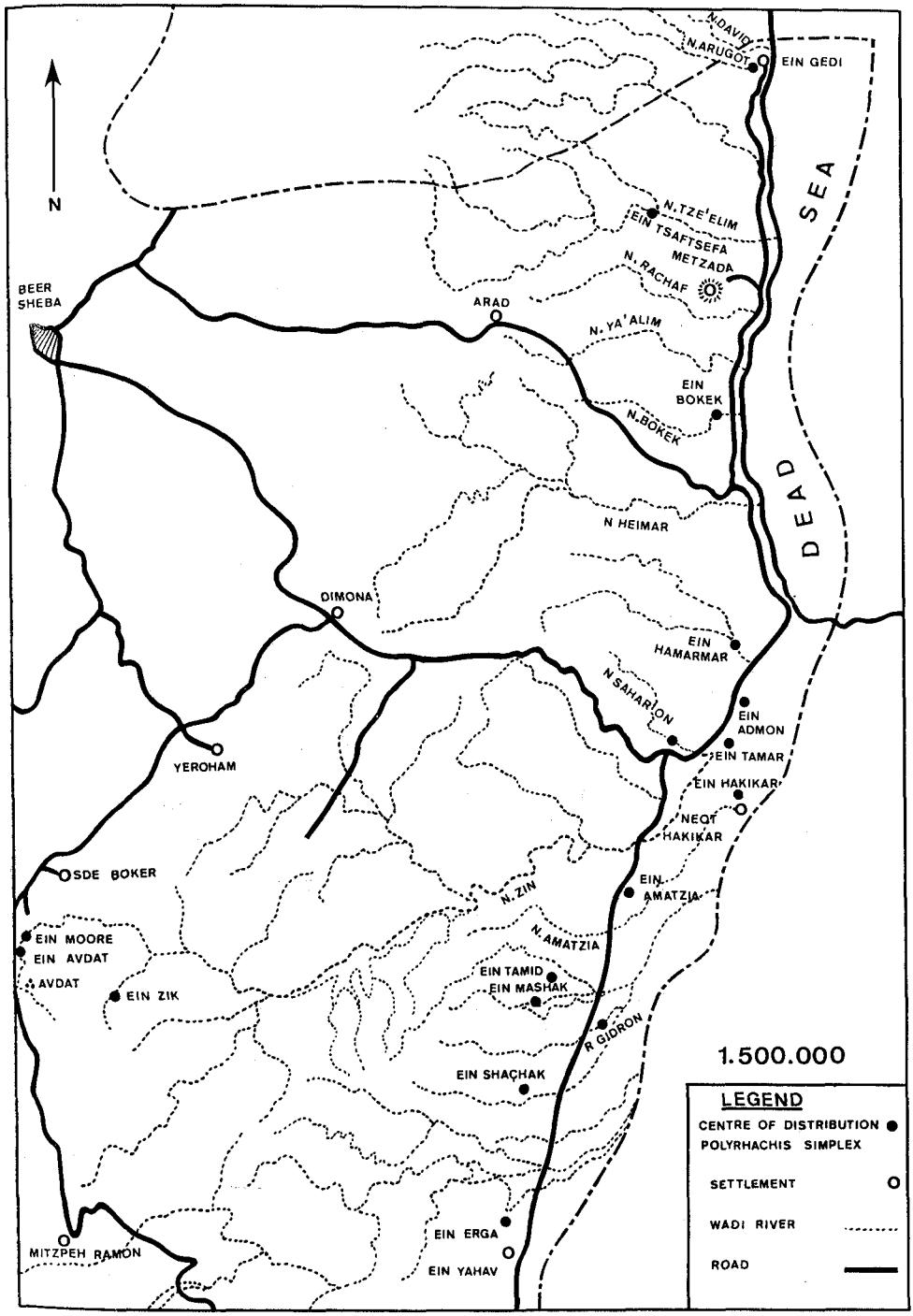


FIG. 8. — Distribution map of *Polyrhachis simplex* in Israel.

also at the other sites (e.g., *Populus euphratica* Oliv., *Tamarix mannifera* Ehr., *Phragmites communis* Trin. and *Arundo donax* L.). Compared to the ant population at the Arugot Stream—hundreds of colonies—those at the other sites are extremely small (a few colonies at the most)—a fact which was established after close scrutiny of the limited area where colonies could be found. The new sites of occurrence of the ants are shown in Figure 8 and are listed below : 1. Ein-Tsaftsefa; 2. Ein-Bokek; 3. Ein-Hamarmar; 4. Ein-Admon; 5. the Saharon Stream; 6. Ein-Hakikar; 7. Ein-Tamar; 8. Ein-Amatzia; 9. Ein-Tamid; 10. The Gidron Stream; 11. Ein-Mashak; 12. Ein-Shachak; 13. Ein-Erga; 14. Ein-Zik; 15. The Avdat Stream.

As can be seen from the distribution map (fig. 8). The range of the weaver ant in Israel does not extend beyond typically desert regions; high temperatures and scattered water sources lend it a tropical character.

## THE BIOTOPE AT THE ARUGOT STREAM : OBSERVATIONS AND MEASUREMENTS

### 1. The temperature

The Arugot Stream is situated in a region in which a desert climate prevails and the temperatures are high all year round. Table I summarises the monthly temperature readings at Kibbutz Ein-Gedi for the year 1964/5 (*). This kibbutz (communal settlement) is located on the southern bank of the Arugot Stream, some 2 km from where the weaver ants are concentrated. During the year, monthly temperature readings were also taken in the immediate vicinity of the ant nests. Comparison of the readings at both sites shows only minute differences, those at the kibbutz being 1-2°C lower than at the nests. The slight discrepancy is attributable to the different topography of the two sites, the kibbutz being more exposed to the regional winds.

Being a tropical ant, *Polyrhachis simplex* prefers high temperatures throughout the year, even when such are available only for a few hours a day. The minimum temperature even during the « cold » months of December-February, is a fairly high 13°C. The maximum temperature in the winter months exceeds 18°C during many hours of the day and since the optimal temperature range (as determined by laboratory observations) for weaver ant activity is 18-28°C, optimal temperatures do occur throughout the year. On the other hand, temperatures above 28°C are extremely unfavourable to the ants, who do not tolerate strong insolation and excessive heat. At such temperatures, activity of the ants is gradually diminished and may come to a complete stop. This occurs especially from June to September, between 10-11 a.m. and 2-3 p.m. (see further under « Ant Migration »). During these warm months, all the ant colonies are concentrated near the stream (among the poplars and reeds), where they benefit from a cooler environment, greater moisture of the ground and a closer proximity to the food sources.

(*) The data are courtesy of the Israel Meteorological Service.

TABLE I. — MONTHLY TEMPERATURE READINGS IN THE REGION OF ARUGOT STREAM DURING 1964-1965

| MONTH | MONTHLY TEMPERATURE IN C° | | |
|---|---|---|---|
| | *Average* | *Minimum* | *Maximum* |
| IX | 30.0 | 25.9 | 34.1 |
| X | 27.7 | 24.0 | 31.4 |
| XI | 22.8 | 17.1 | 28.5 |
| XII | 17.8 | 14.8 | 20.7 |
| I | 15.6 | 13.0 | 18.3 |
| II | 18.0 | 14.5 | 21.5 |
| III | 21.3 | 17.1 | 25.5 |
| IV | 23.1 | 18.5 | 27.7 |
| V | 27.6 | 24.4 | 32.8 |
| VI | 32.8 | 27.8 | 37.8 |
| VII | 32.5 | 27.9 | 37.1 |
| VIII | 32.8 | 29.5 | 37.9 |

## 2. The relative humidity
(Table II).

The relative humidity at the Arugot Stream was measured several times monthly, during 1964/5. The measurements were made at two sites : *a)* A large cliff, some 15 meters from the northern bank of the stream (henceforth called the « cliff »); *b)* an area along the northern bank of the stream. The majority of ant colonies were found to concentrate at both these sites throughout the year. The values given in Table II are averages of the monthly readings. Readings taken at Kibbutz Ein-Gedi

TABLE II. — THE RELATIVE HUMIDITY AT ARUGOT STREAM AND AT KIBBUTZ EIN-GEDI DURING 1964-1965 (AVERAGE MONTHLY READINGS)

| MONTH OF MEASUREMENT | RELATIVE HUMIDITY IN % | |
|---|---|---|
| | *Arugot Stream (average of 3 days each)* | *Ein-Gedi (calculated from daily aberrations)* |
| IX | 47.5 | 43.0 |
| X | 45.0 | 39.5 |
| XI | 50.0 | — |
| XII | 58.0 | 57.9 |
| I | 67.0 | 68.6 |
| II | 58.0 | 51.9 |
| III | 46.0 | 44.9 |
| IV | 43.0 | 40.5 |
| V | 39.0 | 33.4 |
| VI | 43.0 | 34.2 |
| VII | 42.5 | 36.9 |
| VIII | 48.0 | |

during the same year are also presented for purposes of comparison (*). As can be seen from the Table, the region under discussion is an arid one, with a low relative humidity during most months of the year. Except during the winter months (December-February), the relative humidity ranges in the vicinity of 40 %, with minor fluctuations either way. Such low relative humidity is characteristic for the arid region about the Dead Sea. Comparing the relative humidity at the Arugot Stream with that at Kibbutz Ein-Gedi, the former is seen to be higher. The reason for this is that the water and vegetation in and at the stream enrich its atmosphere with water vapours. Moreover, the stream, in some of its larger parts, constitutes a deep ravine which retains its water vapour content and is at the same time subjected to less insolation than the more exposed areas of the region.

## 3. The water

Precipitation at the Arugot Stream is fairly scanty, as can be seen from the following data on rainfall in the area during 1964/5 (courtesy of the Israel Meteorological Service) :—

| *Month* | *Rainfall in mm* |
|---|---|
| December | 22.7 |
| January | 81.5 |
| February | 0.7 |
| March | 9.9 |
| April | 9.5 |
| *Total* | 124.3 |

In fact, the year 1964/5 can be regarded as an especially rainy one for ordinarily the annual precipitation is 70-80 mm. Such precipitation can hardly have any influence on the life of the weaver ant, and its survival in the region is actually due to the presence of active springs all year round The Arugot Stream is a perrenial one and the largest in the area. The rate of flow is up to 180 $m^3$/hr in the winter and up to 160 $m^3$/hr in the summer. Of this hourly amount, Kibbutz Ein-Gedi utilises 100-120 $m^3$; the rest is allowed to flow freely inasmuch as the stream and its flora and fauna constitute a natural preserve. A part of the flow reaches the area colonised by the weaver ants. The water is important to survival of the ants for two reasons : *a)* For drinking purposes; and *b)* for irrigating the growth of Euphratic Poplar *(Populus euphratica)*. Any drop in the rate of flow can kill the poplars and concomitantly lead to annihilation of the weaver ants. Consequently, the problem is receiving much attention from the authorities and last year a first attempt has been made to ensure a constant water supply to the poplars through the use of a sprinkler system. Of particular importance is watering of the poplars during the hot summer months, when there is a drop in the water level of the stream. The results of this initial effort have been promising both with regard to survival of the poplars as well as to activity of the weaver ants.

## 4. Food sources

The diet of the weaver ant is variegated and derived from both plant and animal sources. The vegetal component of the diet includes the Egyptian caper, *Capparis aegyptia* Lam., of the family Capparidaceæ. This bush grows on steep rocks in streams of the Judean Desert (Zohari, 1957). It blooms in the summer and its flower corollas contain much nectar which is lapped up by the weaver ants. The ants are especially attracted to the seeds of the caper, which are covered with a sweet

(*) Readings at Ein-Gedi courtesy of the Israel Meteorological Service.

coating. During the winter and spring, the weaver ants are observed also on the flowers of the Desert Mignonette, *Ochradenus baccatus* Del., of the family Resedaceæ.

The list of food sources of animal origin is considerably larger. The only instance of predation by weaver ants is on midges of the family Chironomidae. These are small, delicate nematocera which fly in swarms near water sources. At the Arugot Stream, they are seen on the leaves of the Euphratic poplar. Owing to their slowness, they are easily captured by the weaver ant, although the latter is not typically a predatory ant.

The corpses of insects are another source of proteins and fats. Those of bees and beetles are consumed on the spot, whereas those of small insects such as flies are carried to the nest. Also collected and carried to the nest are small white masses removed from the excreta of birds and reptiles. As is known, these masses are solidified uric acid which birds and reptiles excrete in their droppings. From this uric acid, the ants obtain salts and various organic materials.

In common with ants of other species one of the primary food sources of the weaver ant is the secretion or honeydew of aphids. That this secretion is utilised extensively is evidenced from the long, crowded columns of ants which lead to aphid concentrations on Euphratic poplars, tamarisks and reeds. Ant traffic to and from the aphids occurs rapidly, with no discernible competetion between members of different colonies. On the other hand, one frequently observes confrontations between two ants during which each commences to probe the other with its antennae. Following such probing, there is a mutual exchange of food which lasts some 2-3 seconds (fig. 9).

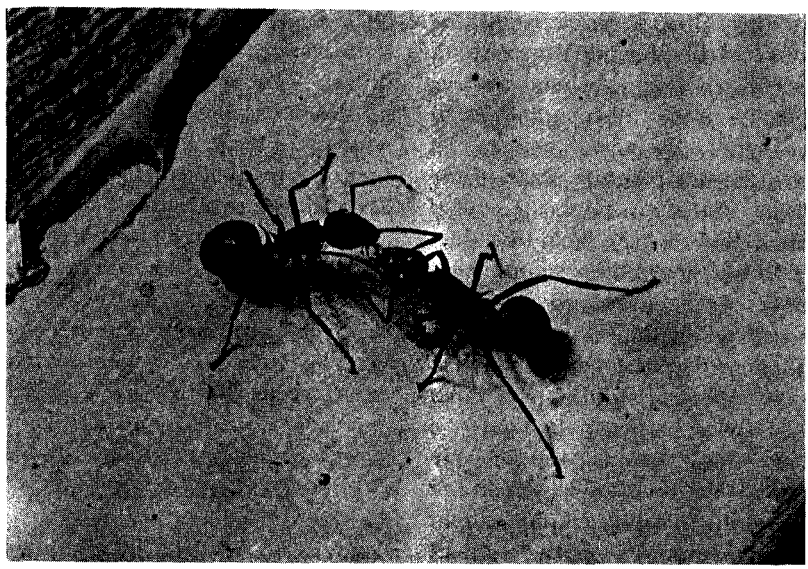

FIG. 9. — Food Exchange between *Polyrhachis simplex* workers.

The weaver ant of Israel visits four species of aphids, two of which are plant-lice (leaf aphids), while the other two are scale-insects or coccids.

THE PLANT-LICE. — These are represented by two species belonging to two different families of the superfamily Aphidoidea (according to AVIDOV, 1961). The first aphid species is *Chaitophorus populialbae* (Boyer) of family Chaitophoridae. Aphids of this species settle in large numbers on the leaves and branches of the Euphratic Poplar (*Populus euphratica* Oliv.; Salicaceae), which serves as a primary host for these aphids at all their distribution sites. This tree attains a heigh of 10-15 meters and being hydrophilic, it is encountered along the banks of the Jordan River, south of Lake Tiberias as well as along streams flowing into the Dead Sea. One such stream is the Arugot Stream. Here, in the vicinity of weaver ant colonies, grow some 20 specimens of Euphratic poplar, some of them 15 meters tall. Throughout the day, during their active period, large numbers of weaver ants can be found covering the leaves and branches of the trees. The ants seek out and crowd about aphid aggregations. The number of aphids in such aggregations ranges between 10 and 60, and the individual aphids are clearly discernible. Most of them lack wings and are of limited mobility only. Aphid populations can be encountered on the poplars all year round. In the winter, however, when the mature leaves fall off, the aphid population dwindles and can then be found only on the young leaves and branches (the young leaves, incidentally, resembling those of the willow tree). In the spring, when the tree blooms, the aphids again spread out over the entire tree-top.

During visits, the weaver ants move slowly through the aphid concentrations and probe with their antennae the tip of the abdomen of individual aphids. From time to time, the ants are seen to pause and ingest a yellowish drop of aphid honeydew. These pauses last 2-3 seconds, and in this fashion the ants proceed methodically from aphid to aphid and from one aphid aggregation to another, till their crop is replete. Engorgement of the ant is clearly discernible from the distension of its abdomen and the spreading apart of the abdominal sclerites.

In addition to the Euphratic poplar, the Pointed Willow (*Salix acmophylla* Boiss.; Salicaceae) may also host small numbers of aphids, but ant migration to this tree is limited.

A second plant-louse visited by weaver ants is the Mealy Almond Aphid, *Hyalopterus pruni* Geoff., of the family Aphididae. The almond Aphid is encountered at the Arugot Stream on the reed hosts *Arundo donax* L. and *Phragmites communis* Trin., both of the family Gramineae. This aphid proliferates on the mentioned reed hosts throughout the year, by means of parthenogenesis and larviposition. The constant presence of the aphids on the reeds is particularly important to the survival of weaver ant colonies in such areas where reeds are the sole hosts of plant-lice.

SCALE-INSECTS. — The scale-insects or coccids in this case belong to the superfamily Neococcidoidea which includes several coccid families, one of which is the family of mealy coccids—the Pseudococcidae. To the latter family belong the two species which provide food for the weaver ant, namely, *Najacoccus serpentinus minor* Green and *Trabutina mannipara* Ehrenb., both of which have a common host tree, namely, the Manna Tamarisk, *Tamarix mannifera*, of family Tamaricaceae.

The second-mentioned coccid (*Trab. mannipara*) is fairly rare and has so far been encountered only at the Arugot Stream, whereas the second is more common. Coccids of both species settle on the young branches of tamarisks in aggregations of 20-30 individuals. Much as in the case of plant-lice inhabiting Euphratic poplars,

here too, the large number of ants visiting the coccids is clear evidence as to the great nutritional value of the coccid secretion. Indeed the ants go to great lengths to protect this food source. Thus, the ants attending *N. serpentinus minor* are instrumental in the construction of a small, silken shelter or « byre » about the coccids, which protect them from insolation. Such « byres » can be seen on tamarisks in the vicinity of weaver ant colonies throughout the year, but in the summer they are even more numerous than at other times because of the increased heat. Their shape may be spherical or saccular ; their size ranges from 2 to 5 cm (in diameter), depending on the number of coccids in the aggregation. The colour of the silken « byre » is the same light brown of tamarisk leaves or of dried plant particles. Each « byre » has one or two entrances through which the ants pass in or out. The silk supply for weaving the « byre » is provided by the late-instar ant larvae. The adult ants transport the larvae from nest to tree exclusively for this purpose, and once the weaving is completed, they are returned to the colony. The weave of the « byre » is sparse and fragile as compared to that of the ant nest « curtain ». « Byres » are constructed also about the plant-lice, but almost exclusively about *Hyalopterus pruni* and not about *Chaitophorus populialbae*. Only in two instances were « byres » observed about the latter species. The reason for this is that *Chaitophorus* is highly mobile and is therefore able to seek its own protection from insolation—by hiding on the underside of the leaves.

Another food source has lately been uncovered at the Arugot Stream, namely, the Humped Cicada, *Oxyrrhachis versicolor* Dist., of family Membracidae. A cluster of 10 cicadas in nymphal stage was observed on one occasion on a tamarisk branch. Surrounding these nymphs were numerous weaver ants who were engaged in lapping up the drops of liquid secreted from the abdominal tips of the nymphs.

## 5. The weaver ant population

As pointed out earlier, the largest concentration of weaver ants is to be fund at the Arugot Stream. The nests of the different colonies are laid out over a narrow belt of land which is 10-20 meters wide and 570 meters long (*).

Direction of flow of the Arugot Stream is eastwards—towards the Dead Sea—and the nests of the weaver ants occur *only* on the northern bank of the stream. Restriction of the nests to the northern bank is probably connected with the fact that the ants require a certain amount of heat to carry out their daily activities and this can only be gotten along the northern bank, which is exposed to insolation at least part of the day; the southern bank, in contrast, lies most of the time in the shade. As added support, there is the fact that the ant colonies extend *along* but not *down* the northern bank. The stream, it should be noted, forms a streep-walled ravine, and the northern wall of the ravine, like the southern wall, is in the shade during most of the day.

The terrain consists mainly of rocks, with an overlay of alluvial soil and pebbles. Various sectors contain numerous cavities which are suitable sites for nest construction, and indeed dozens of nests are scattered over the entire area, some widely dispersed, others—concentrated together. One site is especially prominent in its number of nests per unit area. This parti-

(*) The length, in fact, is not fixed but quite variable, because it is determined by the location of the farthermost nests in either direction and these are subject to change. What is given then is the maximal length observed in the course of the present study.

cular location comprises a massive rocky cliff, some 15-20 meters from the stream proper, which rises to a height of 10 meters above the water surface and extends to a length of 24 meters. This is the previously-mentioned « cliff ». The number of nests on the « cliff » is 80, according to counts made during 1965/6/7. At the foot of the « cliff », there are Euphratic poplars, tamarisks and a dense growth of reeds. The nests are interspersed in cavities close to the surface of the rocks as well as in the soil in front. The density of the nest population is high and occasionally the distance between adjacent nests is merely a few centimeters.

A brief study of the ecological conditions at Arugot Stream quickly reveals the reason why the weaver-ant population here is larger than anywhere else in Israel. The following ecological conditions help to make this site most favourable for development of the ants :

*a)* A large water supply throughout the year, which benefits the ants as well as their host plants.

*b)* A relatively high temperature all year round which never drops below 15° C, and also prolonged insolation during the daytime.

*c)* A rich vegetation bearing plant-lice and coccids as food source for the ants (Euphratic poplars, tamarisks, willows and reeds).

*d)* A topography suitable for the building of ant nests and for seasonal migration.

## 6. The nest of the weaver ant

In its natural habitat, the nest of the weaver ant is hard to detect because it is literally camouflaged. Wherever its location—whether in a cavity or in the litter on the ground—the nest is covered with a silken weave whose outer surface is coated with various debris from the immediate environment, like soil particles, bits of dried plants, etc., thus lending it a colouration similar to that of the environment. What does eventually give away the location of nest is movement of the ants to and from it. The ants enter and leave the nest through a narrow, round aperture, 2-3 mm in diameter.

The aperture is just large enough to allow concurrent passage of two ants. In the majority of cases, the nest has a single entrance, but rarely it may have 2 or even 3 such entrances.

In instances where the nest is located in a cavity, the mouth of the cavity is sealed with a silken « curtain ». The size of the curtain is dependent both on the size of the opening as well as on the size of the ant colony. The side of the curtain facing out is smooth and devoid of any foreign material. The interior of the nest is also padded with smooth silk-stuff of a light brown colour.

The shape of the nest varies in accordance with the shape of the cavity which houses it. Although the nest is not partitioned, forein objects such as a branch or a pebble may at times be encountered inside it and these also receive a coating of silk. The natural nest of a small colony (100 workers) may have a volume of up to 50-60 cc. A colony of the same size under laboratory conditions will have a nest of similar dimensions.

Under conditions in nature, the nests of the weaver ant may be constructed in a wide variety of locations, to wit :

1) Cavities in rocks.
2) Hollows in tree trunks.
3) Among a litter of dry leaves.
4) Under stones.
5) In the ground.
6) On the stem of a tree or bush, near the ground.
7) Underneath the bark of trees.

A common feature of the listed situations is shallowness, that is to say, the nest is never more than 20 cm deep, wherever it is located. Seasonal variations apparently also play some role in the choice of nest locations, for in the winter the majority of nests are located in cavities, whereas in the summer they are found among leaves or pebbles in the vicinity of the stream. This finding will be discussed in greater detail later on (see « Ant Migration »).

disposal prevails both in natural as well as in artificial nests. Coarse wastes, such as the remains of consumed insects or the corpses of dead ants, are carried out of the nest. The latter, however, are not dumped in the regular garbage heap outside the nest but are carried a distance of some 20-30 meters towards the brook, where there is a rocky flat unsuitable for ant habitation. In various depressions or fissures in this rocky flat, one finds large concen-

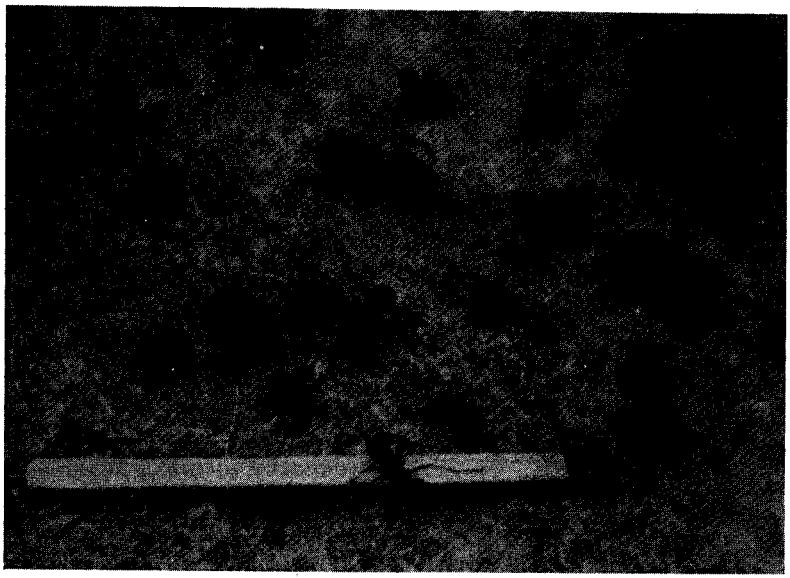

FIG. 10. — « Cemetery » of the Weaver ant on rocky substrate.

## 7. Clealiness in the nest

Open a nest of the weaver ant and the first thing that strikes the eye is the cleanliness inside. The smooth silken weave that pads the interior of the nest further accentuates its cleanliness. Fine waste matter that may occur in the nest is carried to a far corner of the nest and piled in a sort of « garbage dump » partitioned off by a silk curtain. This system of waste

trations of dead weaver ants. These sites merit the name « ant cemeteries » because they contain nothing but the corpses of dead ants, including those of males and queens. In the summer there are more « cemeteries » per unit area than in the winter, because they are not scattered by floods or winds. A typical « cemetery » contains several dozen corpses and extends over an area of 30-60 cm² (fig. 10). From time to time, a « burier » ant can be seen approaching the « cemetery », dragging a

dead ant by one of its legs; she deposits the corpse in the « cemetery » and quickly heads back for the nest. It should be noted that a single « cemetery » serves several different ant colonies.

## 8. Ant migration

It is interesting to note that a seasonal migration of weaver ants, involving a change of nests, occurs twice yearly (in the winter and late spring) near the « cliff » of Arugot Stream. The migration is vertical : from the « cliff » down to the vicinity of the brook in late spring, and vice versa in the winter. The distance of migration is short, being some 10-20 meters. Each migration period lasts for about a month. The winter migration (to the « cliff ») occurs during November-December, and the spring one (from the « cliff »)—during April-May. To study the migration pattern, about 80 ant colonies were selected as subject for observations in 1964/5. On the « cliff » these colonies occupied a small area (about 24 $m^2$) close to the ground (*), which facilitated observations considerably.

In March, during the height of ant activity, the density of population on the « cliff » was about 4 nests per $m^2$. In the summer (May-October), however, the « cliff » was entirely abandoned and the nests were left empty but intact. With the onset of the winter migration (November-December), 60 colonies ascended to the « cliff », comprising about 75 % of the total number of colonies that year. The migrations took place in early morning or in the late afternoon, when the temperature was fairly low and laster for about 3-y hours. The colonies moved in columns and followed a common route. The queens moved on their own power and without the worker « entourage » as typical inside the nest. The workers, in turn, helped to carry other workers, or the pupae and larvae.

Because migrations of the ants were seasonal, it seemed feasible that they were somehow connected with changes in the temperature. To test this theory, the temperature conditions at the Arugot Stream were studied at the previously-mentioned sites of ant colonisation, namely, at the stream bank and at the « cliff ». At the latter situation, temperature readings were taken both on the surface of the « cliff » as well as inside the nests. The temperature readings were taken 10 times a month throughout 1964/5 and were rechecked and found similar during 1965/6. The average monthly temperatures are presented graphically in Figure 11. In view of the fact that the nest temperature readings were practically identical at the streambank and inside the « cliff » cavities, these were combined for the sake of simplification and are presented in the graph by a single dotted line. The temperature readings on the surface of the « cliff » are represented by a dashed line.

As can be seen from the graph, the temperature averages *at* the « cliff » during the winter months range from 17.5°C (in January) to 24°C (in March), which is well within the optimal temperature range for ant activity (18-28°C). However, in the middle of April, the temperatures already approach the upper limit of the optimal, and in May they are well beyond optimum, and it is therefore clear why the « cliff » is abandoned during this period. The ants now migrate towards the stream. Presu-

(*) As pointed out earlier, the nests of weaver ants are built close to the ground. In the present case, the nests were built in cavities in the « cliff » which were never more than one meter above the ground level.

mably, this migration is not so much because of the lower temperatures at the stream—these ar in fact not appreciably lower than at the « cliff »—but rather because of the moisture and the cooling breezes encountered here.

In building their nests at the stream bank, the ants show no preference for any particular habitat. In fact, they may build their summer residences in the litter of dried leaves on the ground, under stones and pebbles or in the hollow of a tree stump. A small number of nests is built on the stems of trees or bushes, close to the ground. Such nests have a saccular shape and attain a length of 8-10 cm.

What brings the ants back to the « cliff » in the winter, or phrased more precisely, what causes the ants to leave the stream bank in the winter ? Again is cannot be temperature alone. Wile it is true that temperature at the stream bank does drop during the winter months, it never falls below optimum, as is clearly seen from figure 11. There is, however, a significant rise in the water-level of the stream and consequently in the moisture of the ground at the area of the nests. Possibly, therefore, these changes are the main reason for the winter migration of the ants.

Returning to fig. 11, it is interesting to note that the curve for « cliff » temperature (dashed line) and the curve for nest temperature (dotted line) intersect twice during the year and in both instances, the intersection coincides with the migration period. Moreover, as we add a third annual curve—the number of colonies on the « cliff » (unbroken line)—to the two already discussed, the three intersect to form two square areas on the graph, each coinciding with the ant migrations. We have thus a graphic demonstration of the connexion between the seasonal activity of the ants and the temperature.

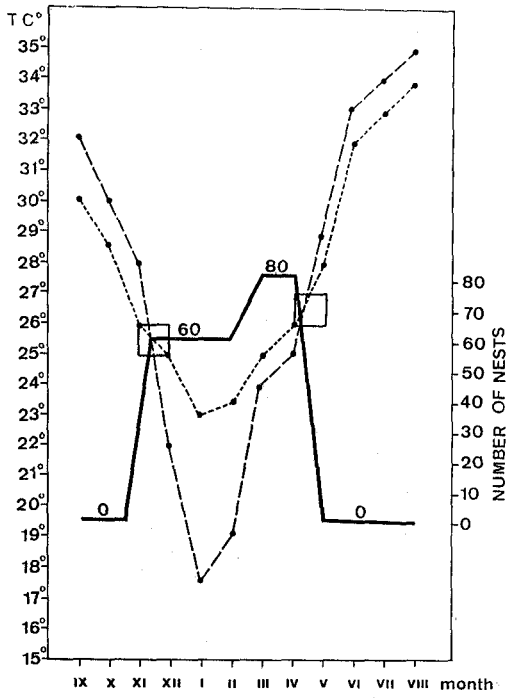


FIG. 11. — Monthly Temperature and Number of *Polyrhachis simplex* Nests as correlated with seasonal Ant migrations at Arugot Stream in 1964/5.

------ Monthly Temperature Readings at the Surface of the « cliff ».

..... Monthly Nest Temperatures (at the stream bank and the « cliff » cavities).

——— Number of *Polyrhachis simplex* nests within « cliff » cavities.

☐ Period of Migration.

## 9. Enemies of the weaver ant

In nature, *Polyrhachis simplex* has but few enemies. The species is active only during the daytime and it is therefore not threatened by insectivorous mammals and reptiles, whose activity in the region of the Dead Sea is strictly nocturnal. The only enemies encountered so far at the Arugot Stream, have been three species of spider, namely, *Pholcus phalangioides* Fissly and *Holocnemus pluchei* Scop., of the family

Pholcidae, and a *Clubiona* sp., of the family Clubionidae. These spiders spread their webs at a distance of 20-60 cm from the ant nests, so that any that strays from the nest becomes easy prey for the spiders.

Under laboratory conditions, however,

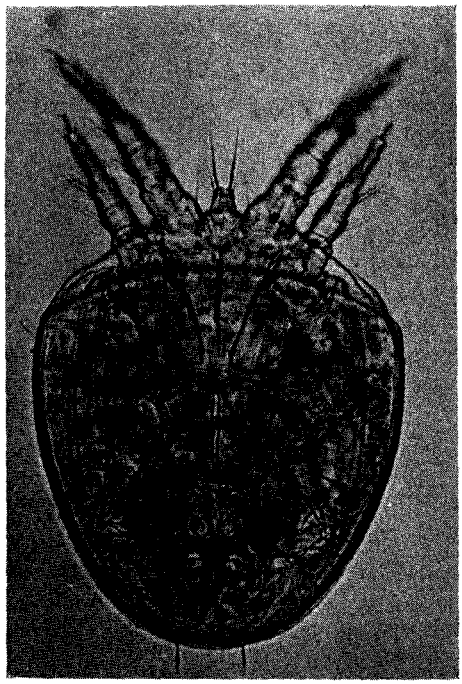

FIG. 12. — Mite Parasite of *Polyrhachis simplex* : microphotograph (400 ×).

another enemy was discovered—an ectoparasitic mite. This mite has been identified as a *Forcellinia* sp.—an ant mite belonging to order Astigmata and the family Tyroglyphiidae (classification according to MICHAEL, 1901). It is about 0.1 mm long and when present on the body of an ant, it appears to the naked eye as a small, ellipsoidal grain of sand (fig. 12). The onset of mite infestation was sudden and there are as yet no clues as to their origin or manner of introduction into the laboratory. Only two facts concerning the mites are certain : *a)* No such mites have been observed on the ants in their natural habitat; *b)* Neither have they been reported on other species of ants in Israel.

Infestation of the laboratory colony occurred gradually. At first, there were but single mites on the bodies of ants and for the most part they attached to the legs and antennae of the ants—organs which come in close contact with the ground. Subsequently, however, their numbers increased from week to week till they virtually covered considerable areas of the abdomen, thorax and head of individual ants. With increasing infestation, behaviour of the ants changed. Whereas previously they carried on normal daily activities inside and outside the nest, in the advanced stages of infestation normal activity was disrupted, probably because of the irritation to such sensitive parts of the body as the mouthparts and the antennae. Infested ants made repeated attempts to dislodge the mites from their antennae and mouthparts, but to no avail, because of the tenacious hold of the mites. The ants became sluggish and hardly moved about. They would stand for long hours in one corner of the nest, without seeking or receiving food. Eventually they died and were rapidly evacuated from the nest by the surviving ants. Needless to say, these mites presented a serious hindrance to laboratory breeding of *Polyrhachis simplex*. In one instance, for example, they succeeded in totally annihilating an active colony of 300-400 workers within a period of 5 months.

## OBSERVATIONS IN THE LABORATORY

### 1. Morphology of the adult

THE WORKER. — *P. simplex* is one of the large ants of Israel. The worker attains a length of 8 mm. From the morphological standpoint, a prominent identifying feature are the three pairs of spines on the dorsal surface of the thorax (fig. 13). The spines of the first pair are located on the pronotum and are short, erect and pointed cephalad. The spines of the second pair are located on the epinotum of the mesothorax; they, too, are erect but are larger and sharper than the previous pair, and are pointed laterally. The spines comprising the third pair are the largest and can be seen with the unaided eye. They are very long and sharp as compared to the others, and are situated on the petiole of the abdomen, together resembling a transverse arc or bow. Upon microscopic examination, a pair of minute, pointed projections may be seen in the space between these two spines, but whether they also contitute spines is rather doubtful.

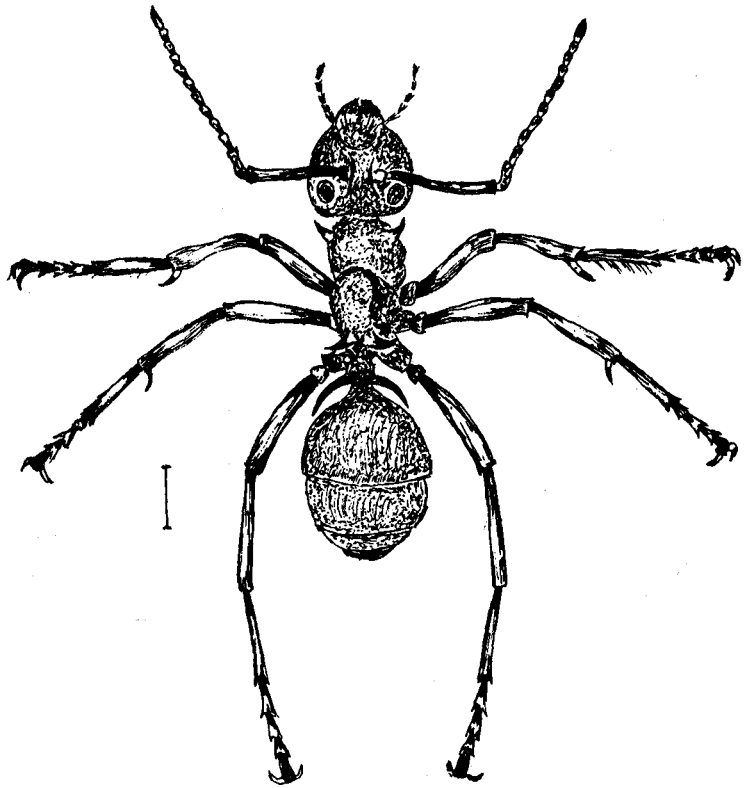

FIG. 13. — Weaver-Ant worker; Dorsal view showing spination (schematic).

The workers are all monomorphic.

THE QUEEN. — Differs but little from the worker. She attains a length of 9.5 mm. The spines on her body are in general shortes—all that remains of the first pair are two minute protuberences, while those of the second and third pairs similar to that in the worker, but shorter.

THE MALE. — Is usually smaller than the queen, its body up to 7.5 mm long. The head is small and the abdomen is pointed, with part of the genitalia showing at the posterior tip. The spines are drastically reduced; in fact, only those of the third pair are discernible and even they are considerably abbreviated.

## 2. Morphology of the larva

Seventeen days after eclosion, the larva commences spinning out its silk. At this age, it is 5 mm long but it attains a length of 7 mm before pupating. The shape of the larva is oval, due to bending of the head. The colour is like that of whitish, opaque glass. The dark-brown mid-gut is conspicuous in the abdominal region and discernible through the transparent integument. The borders of the somites are visible to the naked eye. Under magnification, a thick coating of light-brown hairs is seen over various parts of the body.

On the body of the larva of *P. simplex*, there are 5 types of hair which have been designated by WHEELER and WHEELER (1953) as : 1) branched; 2) simple, short and slightly curved; 3) simple, long and whip-like; 4) denticulate; and 5) uncinate.

Most of the body is covered with short hairs. These are sparse on the head but dense on the thorax and abdomen. The hairs are erect and form a sort of relicate fuzz or « down ». On the dorsal surfaces of the 6 terminal body somites, the long, whip-like hairs are interspersed among the simple short. Additionally, the dorsal surfaces of the penultimate and ultimate somites bear also uncinate hairs, with the hooks anteriorly-directed (fig. 14); there are 8-10 such hairs, equally distributed on the two somites.

As already mentioned, there is considerable variability in the shape of the hairs. The function of the different hairs is not altogether clear. The first four types described, may be reasonably assumed to form a protective, insulating

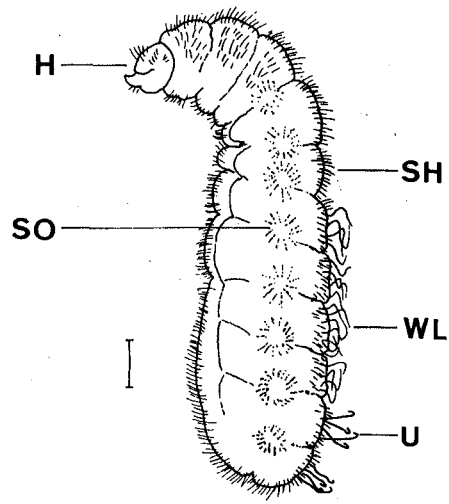


FIG. 14. — Larva of Weaver-Ant (schematic). *h*, head; *sh*, short hairs; *so*, spiracular opening; *u*, uncinate hairs; *wl*, whiplike hairs.

covering on the body of the larva. As for the 5th type, namely, the uncinate hairs, their function is easily enough ascertained by observing the typical resting position of the larva. When in rest, the larva suspends itself head downwards from the silk weave that pads the interior of the nest. Such upside-down dependence of the larva is a very frequent occurrence both in nature as well as under laboratory conditions. Considering the anteriorly-directed tips of the hooks on uncinate hairs, it is clear that their function is to enable the

larva to hook itself upon the wall of the nest (see fig. 15).

The head of the larva is narrow and slightly pointed. On it, may be detected minute antennae (fig. 16). The labrum covers the mouth opening and the mandibles. The latter are composed of brown chitin and are narrow, sharp and slightly serrated on their inner margins. On each side of the mouth is a pair of short maxillary palps. The labium is elongated and protrudes considerably in front of the mouth. At its tip are two pairs of small and anteriorly-pointed labial palps. Between these palps is a narrow, transverse slit—the opening of the silk duct. During the weaving season, the labium of the larva is enlarged due to repletion of the silk duct. Repletion of the silk duct also lends the labium a yellowish colouration, the yellow-hued silk visible through the delicate cuticle of the labium. Along the sides of the body are visible the slightly depressed spiracular openings. At the posterior extremity of the body is a small depression —the anal pore—from which a clear, fluid excretion is occasionally expelled.

Mobility of the larva is limited : only the anterior part of the body, including the head, is capable of slight elevation—which causes the abdomen to protrude forward. Erection of the body is a typical larval posture during the following states : *a)* When begging for food; *b)* When subjected to tactile, photic or other external stimuli; *c)* During weaving; and *d)* During pupation. Such erection of the body also enables the larva to roll itself for a distance of 1-2 cm.

FIG. 15. — Breeding House of *Polyrhachis simplex;* view of the Interior. On the wall—larvae at various instars suspended from the weave, males (winged) and workers. On the Floor—pupae (in cocoons).

## 3. Anatomy of the larval silk system

For obvious reasons, the most important anatomical feature in the larva of the weaver ant is the silk gland. The follow-

ing description is therefore devoted primarily to the anatomy of this organ. In this description, use has been made of JODLOWSKI's (1930) terminology.

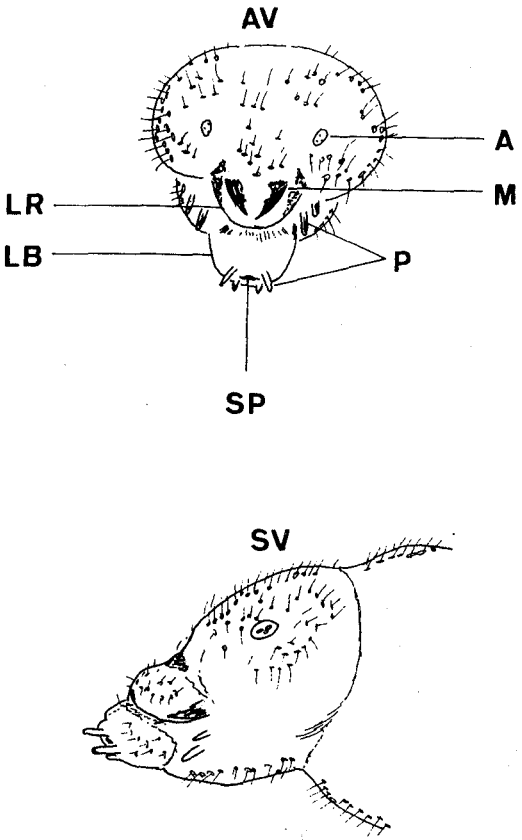


FIG. 16. — Head of Weaver-Ant (schematic). Anterior view (AV) and side view (SV) : *a*, antenna; *lb*, labium; *lr*, labrum; *m*, mandible; *p*, palp.; *sp*, silk pore.

To better study the silk gland or glands of the larva, these were removed in toto under dissection microscope (with magnifications up to 100X). The dissection was carried out in a Petri dish in physiological saline solution. An aqueous 1 % methylene blue solution was found very useful during the dissection insofar as it stained the silk glands a bluish colour and thus made them stand out from the rest of the viscera. As the larva is cut open from the dorsal side, the whitish fat body is revealed and is seen to fill most of the body cavity. Amidst the fat body, the ducts of the silk glands are seen winding in all directions from head to body tip. These ducts are

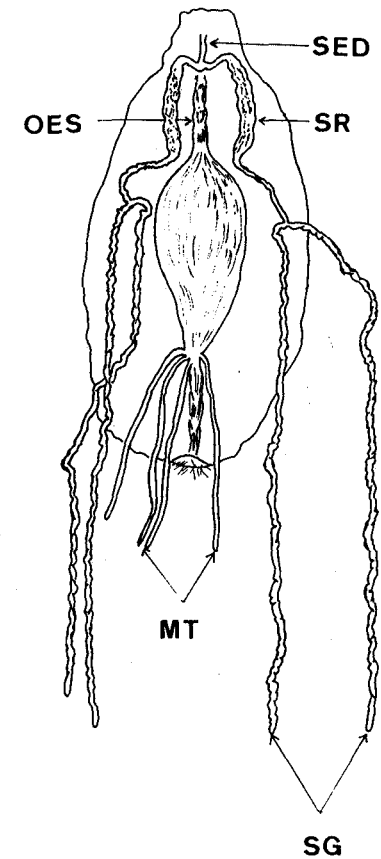


FIG. 17. — Silk Glands of *Polyrhachis simplex* larva (schematic) : *mt.* malpighian tubules; *oes*, oesophagus; *sed*, silk excretory duct; *sg*, silk gland; *sr*, silk reservoir.

thin-walled and therefore expose their yellowish silk content to view. As for the silk glands proper, these comprise 4 rounded tubules whose tips are free of the surrounding tissues. Each tubule is up to 9 mm long

and 0.1-0.2 mm across. The glands lie on both sides of the intestine and somewhat dorsal to it, two glands to each side. The two glands on each side lead anteriorly into a common duct, which is only 1 mm long and similar in structure to the glands proper. The common duct on each side proceeds anteriorly and gradually dilates to a width of 0.3-0.4 mm before emptying into the silk reservoir. The two silk reservoirs, one on each side of the oesophagus, are arched tubes up to 1.5 mm long. They are of a white colour and their walls are longitudinally wrinkled. Histological sections of *P. simplex* larvae reveal the presence of large cells in the walls of the silk reservoirs, which suggests that these reservoirs not only store silk but have some secretory function as well.

In the anterior part of the body, the two reservoirs unite ventrally to the oesophagus to form a common excretory duct. This duct is 0.5 mm long and is not as wide as the silk gland proper. It opens to the outside at the tip of the labium (fig. 17).

To summarise, then, the silk-production apparatus in the larva of the weaver ant is made up of a continuous sequence of tubules and ducts of varying length and width. Within this complex, the three major components are silk glands (4), silk reservoirs (2) and a single excretory duct. The total length of this tube system may be calculated as follows :—

| | |
|---|---|
| 4 silk glands × 9 mm..... | 36 mm |
| 2 silk reservoirs × 2.5 mm.... | 5 mm |
| 1 excretory duct × 0,5 mm.... | 0.5 mm |
| *Total* ..... | 41.5 mm |

Thus the total length of the silk system in the larva is 6 times the length of its body. Such extensive development of the silk-producing organs is clear testimony to their enhanced physiological capacity and indeed enables the larva to spin out its silk for the relatively long period of one week.

## 4. The weaving process and the weave

Under natural conditions, there are two places where the weave of the weaver ant can be easily detected with the naked eye. The first is on the branches of tamarisks, where silken « byres » are woven by the workers to shelter the aphid « cattle », as already described. The second instance are the ant nests which are camouflaged from the outside by a silken « curtain ».

Under laboratory conditions, intentional tearing or cutting by the observer of the nest « curtain », results in considerable agitation of the colony and heightened activity on the part of its members. The initial commotion settles down shortly after, leaving several dozen workers at the nest entrance, to mend the « curtain ». Some of these workers pull the torn edges together, while others haul large larvae from the nest and together they commence weaving at the borders of the « curtain ». The weaving is done as follows : The workers hold the larvae between their mandibles, with the belly of the larva directed towards the « curtain ». The larvae are held by the anterior part of their body at a point about one third the body length from the anterior end. The larva is thus free to move the anterior end. The larva is thus free to move the anterior third of its body in all directions. Holding the larva in this fashion, much the same as, figuratively speaking, a painter would hold a brush the weaving worker moves slowly and cautiously along the torn « curtain », its antennae lightly probing the body of the larva. The latter, in turn, extends and bends the front of its body and periodically touches its mouthparts to the torn area. At each touch of its mouthparts, the larva secretes and fastens onto the « curtain » an extremely fine silk fiber which is invisible to the naked

eye. Thus, the weaving process is seen to be a combined effort, the larva supplying the silk and the weaving worker doing the actual weaving by its movements across the substrate. The number of weaving workers is not fixed. At first only few participate in the weaving, but gradually their number increases to as many as 10. Other workers are engaged in hauling sand particles and bits of plant matter to fasten onto wooden parts or on the glass windows of the breeding house. In a medium-sized colony (400 workers) there are, at times, up to 10 ants weaving concurrently. Silk-secreting ability of the larva commences one week before and continues right up to pupation. Weaving sessions last 5-10 minutes, with long (several hours) pauses in between. There are no fixed weaver ants as such, but rather any worker can tempo-

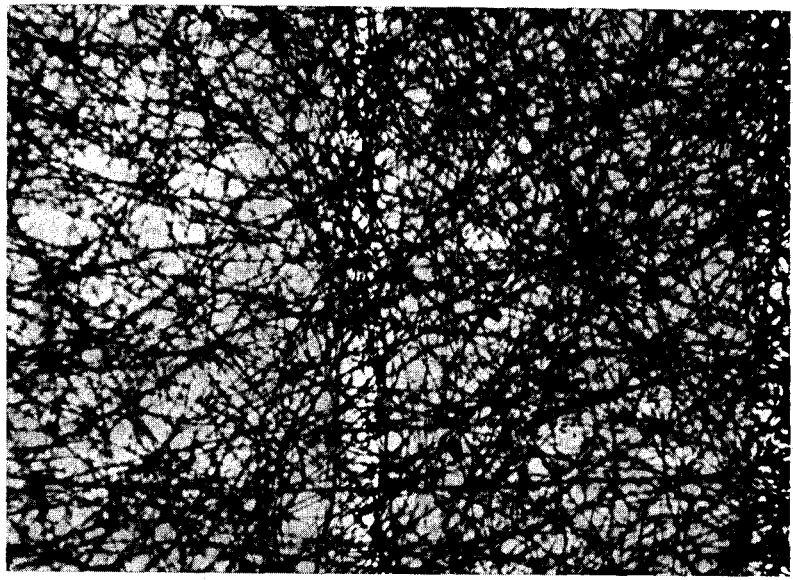

FIG. 18. — The silken Weave of *Polyrhachis simplex* (Photomicrograph 400 ×).

the new weave. The extraneous material is fastened with the aid of the secretion of the worker's mandibular glands.

Weaving is apparently not interrupted during the night, although all activities outside the nest are carried out during the daytime only. In the laboratory, one can encounter weaving activity at any hour of the day or night. Remove one of the shutters of the breeding house and you will find some ants weaving in various parts of the nest—near the entrances, on the rarily assume this role. In a colony in which there are appropriately-sized larvae (5 mm), weaving activities are never interrupted. In such colonies, the weaving is directed initially towards a complete sealing of the nest, leaving just one or two openings to the outside; next, the weavers turn to padding of the interior with many layers of silkstuff. In the artificial breeding houses, silk-coating renders the clear glass windows totally opaque within 2-3 weeks.

Examination of a sample of silk-stuff removed from a natural nest, showed it to be made of 9 closely superposed layers, which suggests that the nest had been occupied and reoccupied at least several times. Stratification of the weave renders it resistant to mechanical damage and helps insulate the colony from the external milieu.

## 5. Chemical composition of the silk

Preliminary chemical characterisation of the silk fibers showed that their main component is a protein. Apart from the protein, there was also a considerable amount of an unidentified inorganic substance, which remained as ash following incineration.

TABLE III. — CHEMICAL COMPOSITION OF *Polyrhachis simplex* SILK AS COMPARED TO THAT OF TWO LEPIDOPTERAN REPRESENTATIVES (own data and those of SCHRÖDER and KAY, 1955).

| AMINO ACID µM/100 mg | *Polyrhachis Simplex* | | | | *Bombyx Mori* | | *Antheraea Pernyi* | |
|---|---|---|---|---|---|---|---|---|
| | Natural Nest Weave | In % | Laboratory Nest Weave | In % | SCHRÖDER and KAY (1955) | In % | SCHRÖDER and KAY (1955) | In % |
| Lysine | 42.60 | 4.08 | 50.50 | 4.06 | 3.85 | 0.30 | 1.14 | 0.09 |
| Histidine | 8.69 | 0.83 | 11.50 | 1.09 | 1.92 | 0.15 | 10.02 | 0.84 |
| Ammonia | — | — | — | — | — | — | — | — |
| Arginine | 24.70 | 2.37 | 23.48 | 2.23 | 5.69 | 0.44 | 31.11 | 2.61 |
| Aspartic acid | 66.80 | 6.41 | 66.70 | 6.34 | 17.62 | 1.37 | 56.64 | 4.76 |
| Threonine | 39.29 | 3.77 | 41.00 | 3.90 | 12.53 | 0.91 | 1.62 | 0.13 |
| Serine | 132.80 | 12.74 | 135.47 | 12.89 | 152.30 | 11.92 | 141.20 | 11.89 |
| Glutamic acid | 124.40 | 11.93 | 123.70 | 11.77 | 11.75 | 0.92 | 9.97 | 0.83 |
| Proline | 26.61 | 2.55 | 22.23 | 2.11 | 5.09 | 0.39 | 3.77 | 0.31 |
| Glycine | 96.80 | 9.28 | 94.87 | 9.02 | 569.00 | 44.54 | 318.90 | 26.85 |
| Alanine | 305.80 | 29.33 | 304.35 | 28.96 | 386.00 | 30.21 | 531.00 | 44.71 |
| Half Cystine | — | — | — | — | 1.43 | 0.11 | — | — |
| Valine | 45.50 | 4.36 | 49.45 | 4.70 | 26.63 | 2.08 | 7.41 | 0.62 |
| Methionine | 5.71 | 0.54 | 6.10 | 0.58 | — | — | — | — |
| Isoleucine | 42.80 | 4.10 | 41.90 | 3.98 | 6.92 | 0.54 | 4.72 | 0.39 |
| Leucine | 55.80 | 5.35 | 55.92 | 5.32 | 6.13 | 0.48 | 4.99 | 0.42 |
| Tyrosine | 9.60 | 0.92 | 9.07 | 0.86 | 62.54 | 4.89 | 58.66 | 4.93 |
| Phénylalanine | 14.40 | 1.38 | 14.45 | 1.37 | 7.96 | 0.62 | 6.47 | 0.54 |
| *Total* | 1,042.30 | | 1,050.69 | | 1,277.36 | | 1,187.62 | |

Viewed under the microscope, the silk-stuff shows an irregular interlacing of its fibers (fig. 18). The individual fibers criss-cross and are glued together at the intersection points. The length of a free silk fiber removed from the edge of the lace-work, is up to 2 mm. The width of the fibers is not uniform, but ranges from 0.7 to 1.0 micron (*).

(*) Measurements courtesy of the Israel Bureau of Standards.

Samples of silk were taken both from the laboratory culture as well as from nests in the field, and it is interesting to note that there were differences in the proportions of protein and ash in the two samples : the sample from the laboratory contained 47.9 % (by weight) protein and 21.3 % ash, whereas that from the field contained 26.4 % protein and 35.9 % ash. There was thus almost twice as much inorganic material in the field sample as in the laboratory one,

which suggests that the material may not be inherent to the fibers but is rather a contaminant which adheres to (or is placed on ?) the moist fibers after they are woven. As for the difference in protein content, there is no ready explanation as yet. Possibly, the abundance of food in the laboratory is a contributing factor.

The protein in the silk fibers was analysed for its amino acids content by the method of SPACKMAN (STEIN and MOORE, 1958). The results of this analysis are presented in Table III, where they are compared with similar analyses from the literature. As can be seen from this Table, the two samples examined (from the field and from the laboratory) have an identical amino acid makeup. As compared to silk from other sources, that of the larva of the weaver ant is poor in sulphur-containing amino acids : methionine is present in trace amount while cystine is absent altogether. As for other amino acids, serine and threonine are also poorly represented, but lysine, arginine, aspartic acid and glutamic acid are abundant. These findings suggest that the larval silk fibers, like those produced by other insects, contain two silk components rich in serine and threonine, and a gum component rich in other amino acids. An attempt to separate off the gum component by heating the fibers in soap or sodium carbonate solution—met with failure.

## 6. Development from egg to imago

In studying metamorphosis of the weaver ant, the observation chamber (fig. 3) proved a most handy piece of equipment. It allowed comfortable and continuous observation under a dissection microscope and could also be easily set up for controlled experiments, where the temperature and food had to be regulated. The following observations on the life-cycle were therefore made with the aid of this chamber.

*a)* DAILY OVIPOSITION OF THE QUEEN. — For the purpose of studying oviposition, a single queen was isolated together with 6 workers for a period of two weeks. With the workers present, the queen was free to concentrate strictly on oviposition. Adaptation of the queen to the chamber was rapid, and already in the first day of isolation she laid two eggs, which were relegated to the care of workers. The eggs are white, elongated and up to 1 mm in length; their surface is sticky and consequently they adhere together in small clumps which are nevertheless easily carried by the nursing worker. The data on ovipositions are summarized in Table IV. As can be seen from this Table, the average daily oviposition during the period of observation was 4 eggs. Minimal oviposition—one egg—occurred on August 24th and August 25 th, whereas the largest daily output—7 eggs—occurred on August 26th and 28th.

*b)* INCUBATION OF THE EGG. — To observe incubation of the eggs, 3 eggs together with 4 workers were introduced into the observation chamber. Despite their isolation, the workers tended the eggs as usual.

During the first week after being laid, the egg exhibits a white, smooth shell. On the 8th day, however, it shrinks somewhat and attains a yellowish hue. With the aid of a binocular, it is possible to follow-up, through the shell, the formation of the embryo till its eclosion 15 days after the oviposition. As pointed out earlier, the surface of the eggs is sticky and so also the emerging larvae, probably because the workers constantly lick both eggs and larvae. With eclosion of the larva, it becomes possible to observe the short, ligth-coloured hairs which cover its body.

TABLE IV. — DAILY OVIPOSITION BY *Polyrhachis simplex* QUEEN

| DATE OF EXAMINATION | AVERAGE TEMP. | MAXIMUM TEMPERATURE (°C) | MINIMUM TEMPERATURE (°C) | NUMBER OF EGGS | AVERAGE FOR 15 DAYS |
|---|---|---|---|---|---|
| 17. 8. 1965 ..... | 27.5 | 31 | 24 | 2 | |
| 18. 8. 1965 ..... | 27 | 31 | 23 | 6 | |
| 19. 8. 1965 ..... | 27 | 29 | 25 | 6 | |
| 20. 8. 1965 ..... | 27.5 | 31 | 24 | 4 | |
| 21. 8. 1965 ..... | 27.5 | 30 | 25 | 5 | |
| 22. 8. 1965 ..... | 27.6 | 31.5 | 24 | 4 | |
| 23. 8. 1965 ..... | 27.5 | 31 | 24 | 2 | |
| 24. 8. 1965 ..... | 27.5 | 31 | 24 | 1 | 4 eggs daily |
| 25. 8. 1965 ..... | 27.5 | 31 | 24 | 1 | |
| 26. 8. 1965 ..... | 27.5 | 31 | 24 | 7 | |
| 27. 8. 1965 ..... | 27 | 31 | 23 | 3 | |
| 28. 8. 1965 ..... | 27.5 | 31 | 24 | 7 | |
| 29. 8. 1965 ..... | 27.5 | 30 | 24 | 4 | |
| 30. 8. 1965 ..... | 25.8 | 29.5 | 22 | 4 | |
| 31. 8. 1965 ..... | 25 | 30 | 20 | 5 | |

*c)* RATE OF LARVAL DEVELOPMENT. — Larval development was studied on 4 larvae which hatched on the same day (July 3rd). This was done to ensure continuity of observations in case one or more of the larvae was injured or killed during the observation period. The 4 larvae were tended by 4 workers. The observations are summarized in Table V, which gives average values of the various measurements. Measurements were carried to one decimal point (0.1 mm), which was considered sufficiently accurate for measuring live, contractile larvae. As can be seen from the Table, development of the larva from eclosion up to but not including the day of pupation, is 23 days. Of interest also are the following facts :

1) The average daily increase in larval length is 0.26 mm.

2) The larva commences spinning out its silk 14-15 days ofter eclosion, at which time it is 5 mm long.

3) Larval growth continues throughout the weaving period.

4) Silk-production lasts for about a week and the weaving activities, although intermittent at first, become increasingly more intensive with the approach of pupation.

5) The larva pupates when 21-22 days old, by which time it already attains a length of 7 mm.

*d)* PUPATION AND PUPA. — While pupating, the larva exhibits mobility as well as flexibility. The larva is capable of so curling its body as to make both ends touch. Its body elasticity allows the larva such freedom of movement within the cocoon as to ensure uniformity of the spinning. Its movements within the forming cocoon are easily discernible through the delicate, transparent weave. Spinning of the cocoon lasts about 24 hours. Two days after the start of pupation, a dark spot forms at one end of the cocoon, which is actually an accumulation of larval faecal material. Length of the pupal case or cocoon is 5.8-7 mm. Development of the pupa was followed up successively in three larvae which had pupated on different dates, so as to ensure validity of the observations. The pupae were isolated in the observation chamber together with a number of workers. Presence of the workers was deemed important for two reasons :

1. To protect the cocoon against parasites, specifically against the book-lice of order

TABLE V. — DAILY GROWTH RATE OF *Polyrhachis simplex* LARVA

| DATE OF EXAMINATION | t° C | | | LENGTH OF LARVA (in mm) | OBSERVED CHANGES |
|---|---|---|---|---|---|
| | MAX. | MIN. | AVERAGE TEMP. | | |
| 3. 7. 1965 | 29 | 24 | 26.5 | 1.2 | Length on eclosion day. |
| 4. 7. 1965 | 30 | 23 | 26.5 | 1.5 | |
| 5. 7. 1965 | 28.5 | 23 | 25.8 | 1.8 | Dark contents seen within intestine. |
| 6. 7. 1965 | 28 | 24 | 26 | 1.8 | |
| 7. 7. 1965 | 31 | 24 | 27.5 | 1.8 | |
| 8. 7. 1965 | 30.5 | 23 | 26.8 | 2.0 | |
| 9. 7. 1965 | 30 | 24 | 27 | 2.4 | |
| 10. 7. 1965 | 30.5 | 22.5 | 26 | 2.7 | |
| 11. 7. 1965 | 30.5 | 22.5 | 26 | 3.3 | |
| 12. 7. 1965 | 30.5 | 22.5 | 26 | 3.3 | |
| 13. 7. 1965 | 28.5 | 22 | 25.3 | 3.5 | |
| 14. 7. 1965 | 28.5 | 22 | 25.3 | 3.7 | |
| 15. 7. 1965 | 29 | 22 | 25.6 | 3.9 | |
| 16. 7. 1965 | 29.5 | 22.5 | 26 | 4.1 | |
| 17. 7. 1965 | 30 | 22 | 26 | 4.4 | |
| 18. 7. 1965 | 29.5 | 23 | 26.3 | 4.5 | |
| 19. 7. 1965 | 30 | 22 | 26 | 5.0 | Onset of weaving. |
| 20. 7. 1965 | 30 | 19.5 | 24.8 | 5.3 | |
| 21. 7. 1965 | 30 | 20.5 | 25.3 | 5.7 | |
| 22. 7. 1965 | 28 | 23.5 | 25.8 | 6.0 | Weaving continued. |
| 23. 7. 1965 | 29.5 | 23 | 26.8 | 6.4 | Weaving continued. |
| 24. 7. 1965 | 30 | 22 | 26 | 6.6 | Weaving continued. |
| 25. 7. 1965 | 28 | 25 | 26.5 | 6.9 | Weaving continued. |
| 26. 7. 1965 | 30.5 | 21 | 25.8 | 7.0 | Pupation. |
| | Average growth | | | 0.26 mm/day | |

Psocoptera. These psocids are common in every breeding house and are usually innocuous, feeding on the organic wastes of the colony. They have, however, been seen to attack and harm the cocoons of pupae which had been separated from the colony.

2. To aid the imago in emerging from the cocoon. The imago ready to eclode is incapable of emerging on its own power, but must be assisted by workers, who help to tear the cocoon from the outside.

Development of the pupa from pupation to eclosion of the adult, lasted exactly three weeks. A few days before eclosion, one could already discern through the wall of the pupal case, darkening of the chitin in the body of the imago. The act of eclosion, assisted from the outside by the workers, lasted about an hour. The emerging imago (a young worker) shows sluggish movement only, and its antennae are contracted.

*e)* DURATION OF METAMORPHOSIS. — The chronology of development from egg to adult is as follows :

(at room temperature from 19.5-30.5°C)

| | |
|---|---|
| Egg development ..... | 15 days |
| Larval development ..... | 24 days |
| Pupal development up to eclosion of the adult from cocoon. | 21 days |
| *Total* ..... | 60 days |

Thus, under laboratory conditions, the duration of metamorphosis is two months

## DISCUSSION

*Polyrhachis simplex* occurs in Israel as a steno-adaptive insect which requires very specific environmental conditions. Among the main requisites for its existence are high temperatures, a constant water supply and aphid-hosting plants. An adverse change in any one of these requisites has a detrimental effect on the size of the weaver-ant population. Ein-Avdat may serve as an example of a site where the temperature condition is unfulfilled. Here water is in abundance and there is also a dense growth of Euphratic poplars, but nevertheless the weaver-ant population numbers a few colonies only. The reason for this is simply that the spring is situated in a deep ravine and consequently the period of insolation is very brief. Additionally, the winter temperatures are lower than usual, the region being 500 meters above sea-level.

To illustrate the importance of water for proper development of the ant population, one can point to the Saharon Stream which suffers from a paucity of water sources. There is a growth of Euphratic poplars and tamarisks near the stream but the weaver-ant population is limited to an occasional colony.

As for food sources, the weaver ant is not strictly dependent on any particular food, neither is it dependent on a particular aphid-hosting plant. Thus, for example, in only half of its distribution sites (the Arugot Stream included), do Euphratic poplars grow; in the remaining sites the weaver ants subsist on the aphids populating reeds or tamarisks.

BODENHEIMER and THEODOR (1929) offer an interesting theory regarding the excretion of the coccid *Trabutina mannipara*, which grows on the Manna tamarisk, *Tamarix mannifera*. They believe the coccid excretion or honeydew to be none other than the manna which the children of Israel consumed as food in their migrations through the Sinai Desert (*). Indeed, the chemical makeup of aphid and coccid honeydew has been keeping several investigators busy during recent years. In the honeydew of the citrus coccid, *Pseudococcus citri* Ris., MOR (1957) detected 10 free amino acids. According to AVIDOV (1961), this species is related to the afore-mentioned *Trabutina mannipara*. IKAN and ISHAY (1966) recognized the following sugars in the honeydew of the aphid *Chaitophorus populialbae* : glucose, fructose, sucrose and melezitose. From the above findings, it is clear that the plant-lice visited by the weaver ant offer it a wide assortment of nutrients and can probably fulfil most of its dietary requirements.

In the morphology of the weaver ant, the spines are an important identifying feature and in fact the generic name of the species implies as much : *Polyrhachis*, as derived from Greek, literally means « many-thorned ». The sub-genus to which it belongs, namely, *Myrmhopla*, also bears reference to the spines, for in Greek « hoplon » means « weapon ».

The specific name of the weaver ant has been a cause for some confusion. According to BINGHAM (1903), the species was first described by MAYER in 1862, who named it *Polyrhachis (Myrmhopla) simplex*. WHEELER (1910 : 217), however, mentions that FOREL calls this species *Polyrhachis spinigera* and indeed FOREL (1923) does employ the specific name *spinigera*, probably to emphasize the spinose appearance of theant. In later publications, however, he reverts to the original name, *P. simplex* and this is the name used also

(*) The fact that species has been given the name *T. mannipara* (i. e., « manna-producing ») by Ehrenberg, suggests that Ehrenberg was also aware of this possibility.

by more recent authors such as MENOZZI (1933), FINZI (1936), WHEELER and WHEELER (1953), BYTINSKI-SALZ (1957) and COLLINGWOOD (1960).

A propos of the weaving, there is need to elucidate the role of the mandibular glands of the worker in this process, for there is controversy in the literature on this point. Thus LEFROY and HOWLETT (1909) apparently do not consider these glands to play any part in the weaving, for they write that after the silk is laid down by the larvae, « ... Other workers bring dry pieces of straw and spread them over the web while it is still fresh. » There is no mention of mandibular glands in their description. FOREL (1923), on the other hand, specifically states that « ... While weaving with their larvae, indeed, ants cannot mingle with their fabric, in a single action, the particles of wood-rot, etc., which they stick together with the secretion of the mandibular glands. These two operations are distinct. »

Observations of the present author tend to support Forel's view. Insofar as the silk dries and hardens soon after being secreted, and whereas deposition on the web of extraneous material is not contiguous with this process, there hardly seems to be any may for the material to adhere to the surface of the web except if to assume that it is glued on with the secretion of the mandibular glands.

The genus *Polyrhachis* contains many species capable of weaving and *P. simplex* is but one of them. In other ant genera, the phenomenon is quite rare. Indeed, apart from genus *Polyrhachis*, only two other ant genera—*Oecophylla* and *Camponotus*—contain weaving species, and these two genera are each represented by a single weaving species only—*O. smaragdina* and *C. senex*, respectively.

The three mentioned genera belong to the same sub-family, namely, to sub-family Formicinae. WHEELER and WHEELER (1953) have the following to say about this subfamily : « The formicinae are generally regarded as the most highly specialized subfamily of ants. » We would go even further. To our mind, the specialization here extends even beyond the ant family, because the role of the larva in this subfamily is unlike that of any other larva. Starting out as a passive, voracious organism, the weaver-ant larva soon transforms into a practically indispensable member of the colony. In supplying the all-important silk and in actively participating in the building of the nest and the aphid « byres », the larva assumes a role which is unique in the animal kingdom.

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